The evolution of modern human diversity

a study of cranial variation

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1 *Introduction*

Modern human diversity is a subject that interests anthropologists and non-anthropologists alike, and most people have a formed opinion as to the scale of diversity existing today. A poll of these opinions among any group of people would most probably reveal greatly disparate views, from those that consider modern human diversity as vast, to those who think of it as relatively small. These different perceptions are explained by the fact that the scale of diversity varies according to the point of reference. Culturally and socially, modern human diversity is indeed vast. The number of social systems, languages, religions, means of subsistence and artistic expression, is so large that a view of a greatly diverse human species is justified. In biological terms, however, modern humans are a relatively homogenous group, as shown by comparisons to closely related species such as chimpanzees. The amount of genetic diversity within a single population of chimpanzees can be greater than that between human populations. This socio-biological paradox has been an important component of socio-historical misunderstandings of the degree of differences between human populations.

Sources of diversity

In order to obtain a measure of the scale of past human diversity and its development different approaches can be used. One of these uses a measure of present diversity, either genetic, morphological, social or linguistic, to establish the degree of relationships between present populations, and through these relationships infer evolutionary patterns. This way of studying the evolution of diversity is essential to provide the framework of population relationships for which an explanation is needed. However, by definition, this method can only work with those populations that exist today or in the very recent past, and even historical records show that a large number of human groups have become extinct. This is also evident when the affinities of many individual modern fossils are assessed and no close relationship to any present modern populations is found. Therefore,

both a framework from recent relationships and degrees of differences and a direct assessment of past diversity through the palaeoanthropological record, human fossils, their material culture and their palaeoenvironmental context, are needed. This shift from real present day parameters to inferential ones requires very strict assumptions to be made, so that human fossils can be taken to represent biological parameters, stone tools and associated assemblages taken to represent socio-cultural context, and palaeoclimatic and ecological reconstructions over broad periods of time taken to represent the sum of the small nuances in environment that influence an individual's life-time. Such assumptions are made by anthropologists and archaeologists every day, and are imbedded in each conclusion and each hypothesis proposed.

However, this exercise is less straightforward than this. All those familiar with palaeoanthropological debates know that many of these discussions are fuelled by researchers speaking past each other in what seem to be different languages. And the analogy to different languages is correct. The moment that anyone interprets the prehistoric record, assumptions are made as to what that record represents. Fossils are interpreted in biological terms, but the biological level may not be the same. One may assume that the differences between two fossil groups represent real genetic differences and thus two taxa, or that they represent adaptations to specific environments within a single taxon, or even that they represent individual variations within a single population. The interpretation of archaeological assemblages is even more difficult, for it encompasses biological and cultural aspects. Elements within an archaeological assemblage may be taken to represent the biological identity of a group, and differences in the record through space and time may be taken to represent population differences and/or migratory movements. Alternatively, archaeological remains may be taken to reflect only the utilisation of resources and environment, and thus differences in the record through space and time would reflect different environmental conditions, social connections, activities, trade routes and raw material. A related problem is whether the differences in material culture should be taken to represent the level of cognition of a population or just the exploitation of available materials within a specific context.

Although in practical terms, the sources of information on the evolution of human diversity can be divided into those that reflect reconstructions from present diversity, for which there is clear evidence and statistically correct sample sizes, and those that reflect past diversity, for which there is patchy but direct evidence, the assumptions necessary to interpret the past would suggest a different division of information. In terms of the inferences

necessary, the fossil data represent biological parameters similar to those of the present genetic and morphological data, and are thus analysed in similar terms. On the other hand, the archaeological data represent socio-cultural information, and with their characteristic horizontal as well as vertical transmission, are thus paralleled by the analytical problems posed by the present distribution of languages and social systems.

Paradigms: continuity and discontinuity

All these assumptions necessary to interpret the prehistoric record are at the root of the debates in palaeoanthropology. They represent the theoretical paradigms within which each researcher works. Therefore, some researchers do not find evidence for biological identity and distinctions in either the fossil or archaeological records, and thus interpret regional records as the result of the continuous temporal change of a single population. Also, there are those researchers that identify different populations in the morphological and archaeological differences they observe, and thus interpret regional records as discontinuous and characterised by population turn-over. These differences in paradigms in palaeoanthropological research are not unique to our subject, and reflect a more general debate on the gradualism of the evolutionary process.

However, besides the issue of gradual versus punctuated change in evolution, there is the question of universality of mechanism. It is likely that all possible different interpretations mentioned above (and many more!) probably apply to different hominid groups at different times in different contexts. There is no reason to believe that the same conceptual biological and social parameters, i.e. a single paradigm, apply to different hominids or even to different populations of a hominid species. Within the dynamics of the evolution of populations, the demographic and environmental conditions will determine the character of the record, and define the changes in a population as continuous or discontinuous, local or migratory, resulting in speciation or subspeciation events.

The issue of modern origins and origins of diversity

The research presented in this book arises from this problem of gradualism and universality in the interpretation of the evolution of modern populations. It tackles two main questions, that of the origins of modern humans from an archaic ancestor and the origins of the differences between modern

populations. Depending on the evolutionary perspective, these issues may or may not be coupled together.

If a gradual and continuous view of modern human origins is assumed, then the regional differences between populations are related to the first establishment of widely dispersed regional hominid groups, whether modern or archaic, for it is assumed that regional continuity of occupation and form occurred. This view has been formulated into an evolutionary hypothesis called the Multiregional Model of modern human origins. It argues that there was no event associated with the appearance of a modern human form, but rather the development of regional variants of a single species which followed similar evolutionary trends because of extensive inter-regional gene flow. The establishment of regional variants would have occurred approximately one million years ago, when *Homo erectus* expanded out of Africa towards Southeast Asia, Eastern Asia, Central Asia and Europe, while the transition from archaic to modern would have occurred in parallel in all regions because of genetic diffusion. According to this view, a modern human morphology is secondary to regional diversity, and thus, the origin of human diversity precedes the origin of modern humans. The first section of this book explores a multiregional perspective of origins, both of humans and human diversity.

An alternative view would see the record as discontinuous and anachronic, and interprets the appearance of modern humans as a distinct localised event followed by replacement of archaic hominids. This view has also been formalised into an evolutionary model of origins, called the Out of Africa hypothesis. It argues that modern humans appeared in Africa in the late Middle to early Upper Pleistocene, and subsequently expanded to form regional populations which diversified from an already modern ancestral form. According to this view, modern human regional diversity is secondary to a modern morphology, and thus, the origin of modern humans precedes the origin of modern diversity. This view is explored in the second section of this book, in which evidence for a distinct event leading to the appearance of modern humans in Africa, significantly earlier than in other regions of the world, is discussed. In interpreting the apparent discontinuity in the record as supporting a single and recent origin of modern humans, the temporally and spatially variable character of the later modern human regional record is developed further into a model of multiple events starting from a single ancestral source and multiple evolutionary mechanisms that may account for the non-universality of process.

The key to this argument lies in the role of gene flow between regional populations of archaic and modern hominids. Besides temporal regional

continuity, a multiregional model of Pleistocene hominid evolution requires that large amounts of spatial continuity between regions took place. This large amount of genetic exchange between widely separated areas like Java, East Africa, Europe and China, is necessary in order to maintain the temporal overall similarities and prevent local speciation occuring. Again, past gene flow cannot be directly measured, and traditionally two sources of inferential information have been used. The first of these is inferred from current genetic exchange between foraging groups like the Inuits, and transposed into the past. This method gives a good measure of possible gene flow in hunter–gathering groups, but does not take into account past demography and the opening and closing of routes in the past million years. Whether the world population of *H. erectus* had the necessary critical size to maintain gene flow patterns similar to any modern group is again debatable, and current interpretations of mtDNA data suggest not. The second source of evidence for inter-regional gene flow comes from the appearance of fossils and/or archaeological remains in one area which have strong affinities with another region of the world. These new forms are interpreted as resulting from gene flow from another regional hominid population, which acts to maintain the gradual multiregional change through time. However, this interpretation is again part of the paradigm of gradualism and continuity, and an alternative punctuated event leading to the migration of new forms into an area and eventual replacement of the original local inhabitants is also possible.

The question of replacement

The issue of whether gradual and universal mechanisms characterise the evolution of modern populations also has a socio-political dimension. It has been argued that the view of punctuated and rapid events creating discontinuity of populations (i.e. population extinction) is a 'racist' view of prehistory, one that highlights the supremacy of one form over the other (be it modern humans over Neanderthals, or one modern population over a previously existing one). However, the question of evolutionary advantages of one group in relation to other closely related groups or even individuals is the whole basis of Darwinian thought. That the observed succession of forms in the fossil record represents the advantage of one form over another is the reality of evolution. This advantage may be biological, social, demographic, or even incidental, in the sense that a population may out-compete another only for the particular circumstances (environmental or demographic) of the moment in which they are competing for resources

rather than for an absolute biological or social advantage. In such cases, the replacement mechanism may be reversed as circumstances change. A good example of such a mechanism is provided by the alternation of modern and Neanderthal forms in the Middle East during the Upper Pleistocene. It is probable that early modern humans had neither a biological nor a technological advantage over early Neanderthals, as shown by the fact that early modern humans did not expand into Europe during the last interglacial. Therefore, the alternate occupation of the Middle East (an area that suffers strong climatic changes during interglacial and early glacial conditions through the northward and southward displacements of African and Asian climatic regimes) by early moderns and Neanderthals may only reflect circumstantial environmental conditions favouring one or other subsistence adaptation, rather than a real bio-social advantage of one group over the other. However, even in these circumstantial cases, replacement does take place. Evolution results in population replacement through time, as new forms pass to occupy the area previously inhabited by another group of similar niche when biological, social or environmental conditions change.

However, these replacements as seen on a geological time-scale may be real or an artefact of the record. It is possible that a change of fauna in the history of a region represents a real replacement event, by which a new form (locally evolved or migrant) will out-compete a resident population. The only clue for such an event would be evidence of a four-stage sequence: (1) the presence of a single population in an area, or one that forms the vast majority; (2) the appearance of a new form, or the increase in numbers of a minor group; (3) a period of contemporaneity of the two groups; and (4) the disappearance or strong reduction of the first population. However, incomplete replacements, i.e. when the new population becomes the great majority but not the only group in the area, imply the formation of small isolated pockets where evolutionary relics of the earlier form can survive. Such pockets result from either geographical refugia (i.e. areas where the new group does not reach) or ecological refugia (i.e. areas where the conditions are so stable that the existing adaptations of the early form are not out-competed by the expanding group). The first relates to geographical barriers, while the second to stability of the niche. Again, both these situations are realities of animal evolution, and examples of the persistence of evolutionary relics, in isolation or exploiting specific ecological niches, abound. The existence of these relics, for whatever length of time, are evidence of the non-universality of events. However, there is yet another mode of change of population through time that may seem to take the form of population replacement as in the first case, but is not. That is the case of

extinction of regional populations, for reasons not related to competition or contact with closely related groups, followed by later occupation of that area by a new related form. In this case, actual replacement of one population by another did not occur, but only as an artefact of the geological scale of palaeontology.

In the history of modern humans, evidence for all these modes of replacement can be found. The turn-over from a Neanderthal to a modern population in Europe between 40 and 30 ka (thousand years) ago is an example of the first mode. The Neanderthals were the regional population of Europe until the first modern forms appear in the record just before 40 ka. A period of contemporaneity follows, and later only modern humans are found in the area. Geographical relics of Neanderthals existed in certain areas, like southern Spain, for some time. This replacement process does not rule out population admixture, that may have occurred to greater or lesser degrees, but never to the extent of creating a population of equal Neanderthal and modern affinities. Replacement events with the formation of geographical and/or ecological relics abound in the history of modern populations, and the recent expansions of agricultural groups, with the persistence of foraging communities in small numbers, is only one example. The third mode of replacement, the artefactual one, may be represented in Southeast Asia. It has been traditionally assumed that evolutionary continuity from Javanese late *Homo erectus* to Southeast Asian and Australian modern humans took place, and suggestions to the contrary imply replacement of these late archaic Javanese forms. However, the age of the last *H. erectus* in Southeast Asia is uncertain, possibly last interglacial but possibly earlier. There is no fossil or archaeological record in the area to suggest that this population was still there 50 thousand years later (at least) to be replaced by early modern humans. In this case, the occupation of the area by modern people would seem to have replaced an earlier archaic group, but separated by a period of time during which the area may have been uninhabited.

Continuity of occupation

This brings us to the question of continuity of occupation. Hominids have had an almost world-wide geographical range for at least a million years (excluding Australia, the Americas, high altitudes and the Siberian plains). The capacity of exploration, exploitation and expansion of *Homo erectus,* evidenced by this world expansion, is one of the reasons for assuming that, once it had been colonised, an area would be continuously

occupied by hominids. This is an assumption that is difficult to test with the palaeoanthropological record. In some areas the archaeological record is sufficiently rich as to allow some measure of stability of occupation, although the scale of measurement in terms of hundreds, thousands or tens of thousands of years defies assertions of continuity in the generational scale needed for evolutionary continuity to take place. However, other areas lack such archaeological record and have instead sporadic fossils to attest to hominid presence in the region. Such an area is Java, where stone tools are largely absent but from where hominid remains dated to before one million years, approximately 700 ka and 100 ka ago, have been interpreted as reflecting continuous occupation. The continuity of occupation of Java is very possible, but certainly not proven by the available record.

The question lies in the stability of hominid populations and the interaction with unstable environmental conditions. That most hominids identified in the Pleistocene fossil record were at one point successfully adapted to their particular region of the world there is little doubt. However, biological and non-biological components of all environments are continuously changing, and with a wider spectrum during the climatic fluctuations of glacial cycles. Such drastically changing conditions that brought about extremely arid and cold phases, interrupted by short episodes of wet and warm conditions, must have affected the availability of resources within any one area. Furthermore, the scale of climatic change in the Pleistocene formed and destroyed geographical barriers, intermittently bringing normally allopatric animal and human populations into contact with each other. These changing conditions must have implied changing strategies in subsistence foraging, resulting in either more densely and localised or more thinly and widely distributed populations. These demographic fluctuations in terms of population numbers, density and range, are at the root of the problem of continuity of occupation.

Although it is not possible to obtain realistic measures of palaeodemography in many situations (like the case of Java mentioned above), the comparatively rich Upper Pleistocene record shows that such fluctuations were a fact of human history. The reconstruction of the late archaeological history of certain areas with rich records, like Europe, Australia and South Africa, clearly show that during specific periods of time parts of these areas were virtually uninhabited. In the case of Europe, the northern plains were depopulated for a short interval during the last glacial maximum, giving rise to very dense occupation of southwestern Europe and temporal discontinuity with Italy and central Europe. In Australia, the extremely arid conditions of the last glacial maximum also had a

demographic effect, giving rise to a period of population refugia during which some groups could have become extinct. In South Africa, as in pleniglacial northern Europe, the archaeological record also points to depopulation, but this seems to have preceded the glacial maximum by some 20 ka.

These few examples of late Pleistocene fluctuations in demographic patterns show that not only the process of evolution of populations is a dynamic one, but that it is very circumstantial in nature. Macroclimatic events seem to have affected regional populations in different ways and to a different extent, while the same regional population seems to have responded differently at different times to events of apparent similar scale and extent. The circumstantial determinants of the evolutionary process that make a population expand, contract or change in response to a particular environment at a particular time, are the source of the anachronical spatial patterns in the palaeoanthropological record.

Multiple events and the universality of process

In the course of the last few decades, palaeoanthropologists have come to see major events in hominid evolution as independent – bipedalism, tool use, brain expansion, life-history, language and many more. It is even accepted that the earliest hominids share with African apes important aspects of biology, such as size, life-history and probably cognition, although their habitual posture allies them with our own family. The same principle of independence of events should be applied to the late Pleistocene. It is necessary to decouple events in order to establish the patterns and allow the interpretation of process. In the study of modern human origins and diversity, the events relate to biological and social spheres. I started this introduction by saying that the extent of modern diversity in one sphere is far greater than the other. To this we should add that the temporal changes in any one of these spheres may not have been universal or synchronous across the range of modern human populations in the past or even the present.

Disclosing human diversity requires the establishment of the evolutionary patterns and processes, while understanding diversity requires the investigation of biosocial adaptations and demography. This book is mainly concerned with disclosing the evolutionary patterns and processes that gave rise to modern human diversity, although genetico-demographical parameters are briefly discussed in order to establish regional mechanisms. By proposing a model for the evolution of modern human diversity from an ancestral source, this book offers a theoretical framework with which to

work towards an understanding of the biosocial parameters of each past population that created the stability or instability of past human occupation, and thus the character of the evolutionary patterns and processes that gave rise to modern human diversity.